

PRESIDENTIAL ADDRESS

The Phylogenetic Significance of *Dracaena*-type Growth

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Edited from the author's notes by C. J. Quinn*

The lilies, as we know from an old comment, are arrayed in more glory than ever was Solomon. In spite of their glory which, to a modern taxonomist is but a manifestation of character-states, the lilies seem to be awaiting someone with the wisdom of Solomon to find themselves classified. Of course I use the name 'lily' rather extravagantly; in a strict recourse to nomenclature the family taxon, Liliaceae, must accept the genus *Lilium*. But the problems seem to be: what other genera might be placed with *Lilium* in the family of lilies, and which other families have, say, an ordinal relationship with the lilies?

In this comment to-night I am not going to delay with the history of the convolutions in the classification of these Monocotyledons, but the historical candidates for the Liliaceae have flowers that may be derived from a trimerous 5-whorled condition $P_{3+3} A_{3+3} G_{(3)}$. The ovary may be superior or inferior, and a whorl of stamens is sometimes missing.

Amongst the various taxonomic treatments of these candidates for the Liliaceae we can for the moment note that:

Brongniart (1813)	disposed them in several families, including Liliaceae
and Lindley (1846)	and Amaryllidaceae;
Engler (1897)	grouped them in a few big families;
Hutchinson (1934)	allocated them to many families in several orders (Liliales, Agavales, Amaryllidales and Haemodiales pp.);
Cronquist (1968)	has more recently become confused and has gone back to some larger-than-Engler families in a single order, Liliales;
Huber (1969) and Dahlgren and Clifford (1982)	who are enjoying some present day popularity, have lots of small families arranged in several orders (e.g., Liliales, Asparagales, Amaryllidales and Haemodiales pp.).

The differences in the above systems are not the simple matter of tribes being elevated to families and families becoming orders, for an inspection shows the content and alliances keep altering. Hence we are faced with a real systematic problem, which indicates that we have been doing something wrong — wrong in the sense that wide

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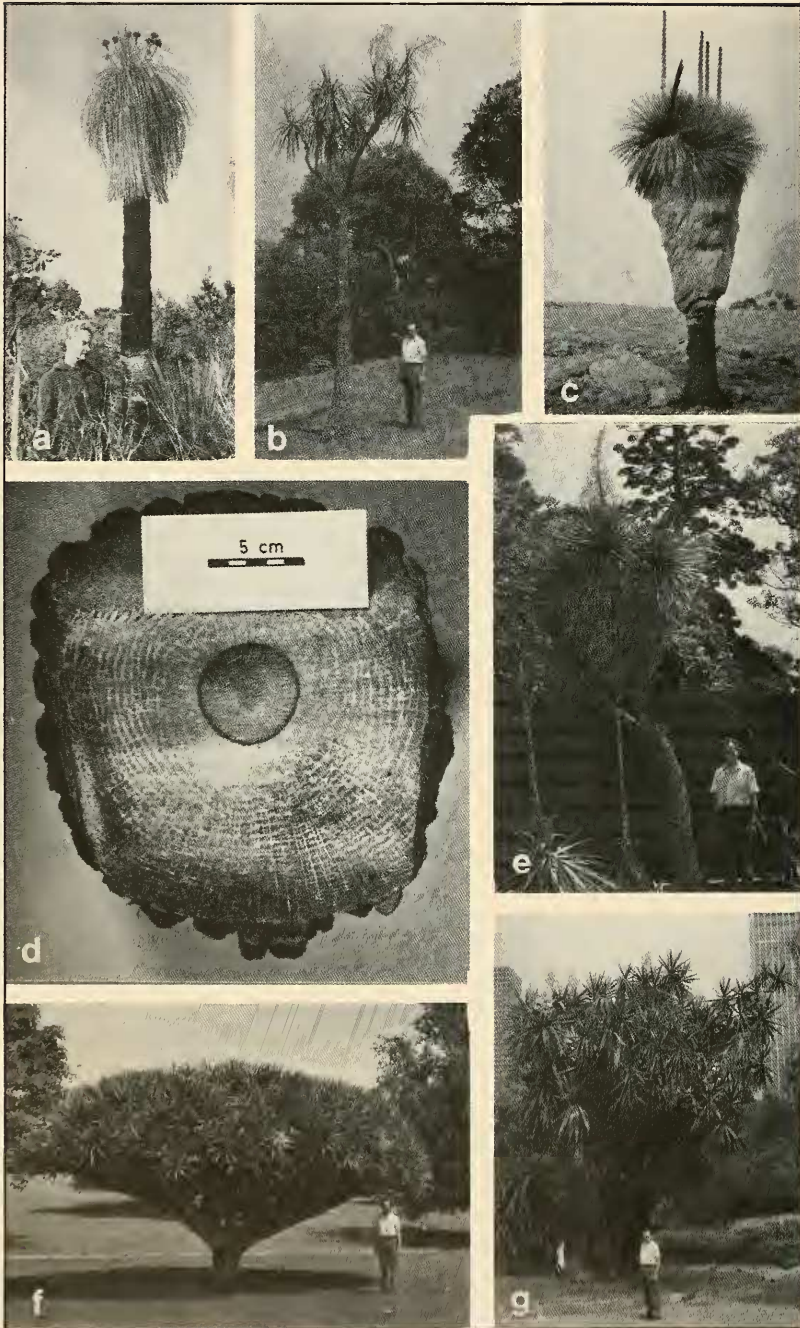


Fig. 1. Examples of pachycaulous monocotyledons.

a. *Kingia australis* with post-anthetic inflorescences: Albany, Western Australia. b. *Beaucania* sp. c. *Xanthorrhoea reflexa*; box at base of trunk is 15cm high; Beverley Western Australia. d. Transverse section of 1.9m high *Xanthorrhoea arborea* trunk at ground level. The primary tissues, including the basal woody cone, occupy the central region to a diameter of 8.5cm; the remainder of the trunk is secondary, arising from a perimeristem that is under the dark outer layer of leaf bases and bark (see Fig. 2a). Calga, NSW. e. *Yucca elephantipes*. f. *Dracaena draco*. g. *Nolina* sp. b and e-g, Royal Botanic Gardens, Sydney.

acceptance or approval is not being given to any one system. What is it we are doing wrong?

Now, one of the features of natural classification is that if we use the character-states of A, B and C to set up family number 1, we see no necessity to use another set of character-states of A, B and C to set up family number 2. It is, however, a fact of taxonomic history that character-states of the flower have, by and large, been used very successfully in setting up families and supra-specific taxa in the dicotyledons. Of course we have seen plenty of tidying up with input from more recently available data sources such as histology, karyology, biochemistry, palynology. But the tidying up was often already seen to be required. There are indeed also many monocotyledonous taxa of wide and long-time acceptance that can be well circumscribed on floral character-states.

It seems, therefore, that, following the comparative success of floral characters in the classification of most dicotyledons and many monocotyledons, we have expected the same approach to be successful over-all. This expectation, I believe, should be abandoned with reference to the Lilies and their relatives. I have come to this opinion as a result of some studies contemplating the Australian family Xanthorrhoeaceae, which consists of genera that have all been considered at some time or another candidates for the Liliaceae. The Xanthorrhoeaceae (in its present content) was set up by Hutchinson (1934), whose system for the 'lilies' in particular presented some novelty, in that attention was paid to non-floral characters — habit and leaves — as well as to floral characters, in setting up the numerous families and orders.

Hutchinson's Xanthorrhoeaceae contained genera with species of gross habit — small trees or 'shrubs' (as far as these terms can be applied to monocots; Fig. 1a, c). It included, *inter alia*, the three genera, *Xanthorrhoea* (ca 15 spp.), *Kingia* (1 sp.) and *Dasyopogon* (2 spp.), and he put this family in the order Agavales along with his family Agavaceae, which again contained species of gross habit (Fig. 1b, e-g) belonging to such genera as *Dracaena*, *Cordyline*, *Doryanthes*, *Yucca*, *Phormium* and *Nolina*. In both families, therefore, there are species which can be described as arborescent or at least frutescent — in general, pachycaulous; so in this complex — Hutchinson's Agavales — we are dealing with big perennial robust monocotyledons with a habit that probably impressed a botanist of the northern hemisphere where monocotyledons are spring-flowering shoots produced annually from bulbs, corms and rhizomes.

In the development of a natural classification it has forever been unwise to fasten on to one character-state for setting up a taxon. Moreover, such a character-state distributed in representatives of that taxon must be seen as an homologous expression of a character. Thus, is it reasonable to postulate that *pachycauly* in Hutchinson's Xanthorrhoeaceae and Agavaceae is the result of homologous developmental processes in all the genera/species referred here?

Some years ago I started to investigate this point. It was relatively simple to show that the pachycaulous habit in members of the Xanthorrhoeaceae is the expression of two fundamentally different processes. In the course of the studies it also became obvious that Hutchinson's character of 'dry perianth' as typical of the family is also questionable; this uncertainty ultimately led to an investigation of the floral anatomy of some of the members of the family. The precise results of these investigations are to be published in full later. For the present, and to be succinct, Hutchinson's family Xanthorrhoeaceae is monstrously unnatural. However, as a result of these studies I consider there are two histological aspects in the 'lilies' (? and indeed in other monocots) that are of systematic importance:

- i) features associated with the development of pachycauly; and
- ii) features of the ovary wall — especially the septa.

In searching through the literature I note that there is nothing particularly novel about the features I am going to describe; it is simply that their systematic importance has not been highlighted. Moreover, the details are fairly well recorded, so I can only conclude that as systematists we are ignoring a whole pool of histological data already scored by various workers.

Regarding pachycauly, the kind of development I wish to consider tonight is that kind found in species of *Dracaena*. I am going to imply that other kinds of pachycauly in monocotyledons are very different (e.g., that in *Kingia*; Fig. 1a), though I am not going to describe them to you (see Staff and Waterhouse 1981). As you can see from the illustrations (Fig. 1b-g), many of the species that have the Dracaenoid kind of pachycauly are quite arborescent.

The basic histological processes producing this type of pachycauly have been known for a long time (since 1840-1870), but they really are not given much attention in accounts of general plant histology, and, if mentioned at all, the histological picture is usually described only in the transverse aspect of the stem, whereas it is in the longitudinal aspect that some of the most interesting and fundamental features of the process are to be seen.

In the transverse aspect of the primary stem (Fig. 2d) I want you to note:

- a) the scattered vascular bundles, a typical monocotyledonous character; all tissues are of course primary;
- b) that the vascular bundles are cribricentric, or nearly so, a feature found in, but not widespread in, monocotyledons;
- c) that the tracheary elements are tracheids and the metaxylem ones have oblique narrow-aperture pits, features found in, but again not widespread in monocotyledons (these features are of course only ascertainable in macerated tissue);
- d) the peripheral cylinder of meristematic cells, which is probably more than one cell thick.

The transverse aspect of a stem with secondary thickening is shown in Figs 1d and

2a. The points to note are:

- a) the perimeristem cuts off radial rows of parenchyma cells to the inside and a few to the outside; these are appropriately termed secondary tissue;
- b) proceeding centrally from the perimeristem —

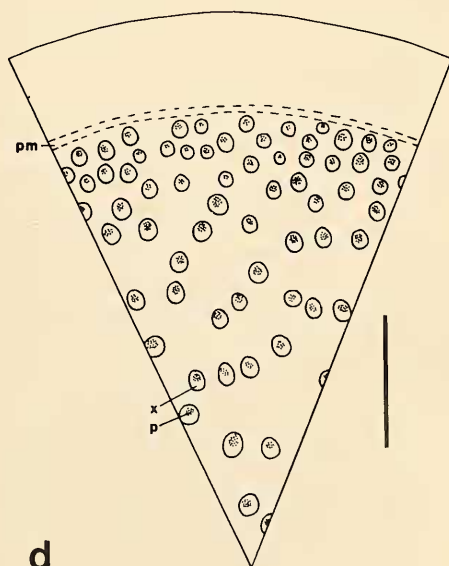
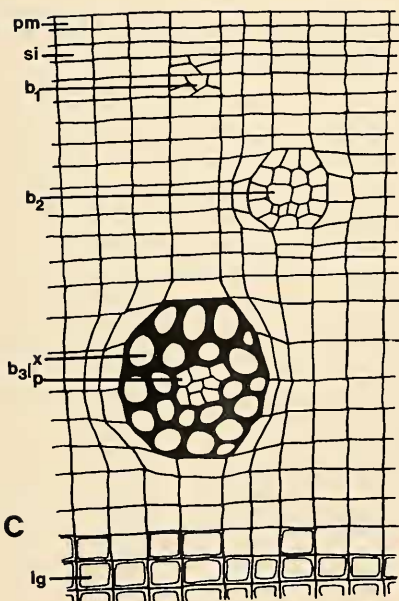
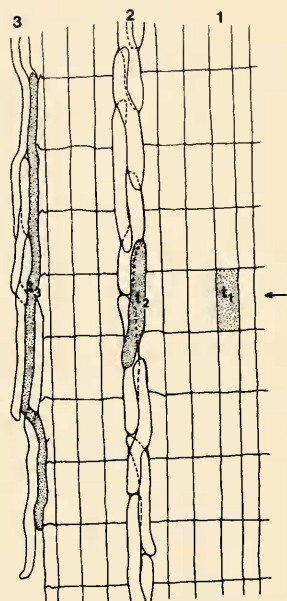
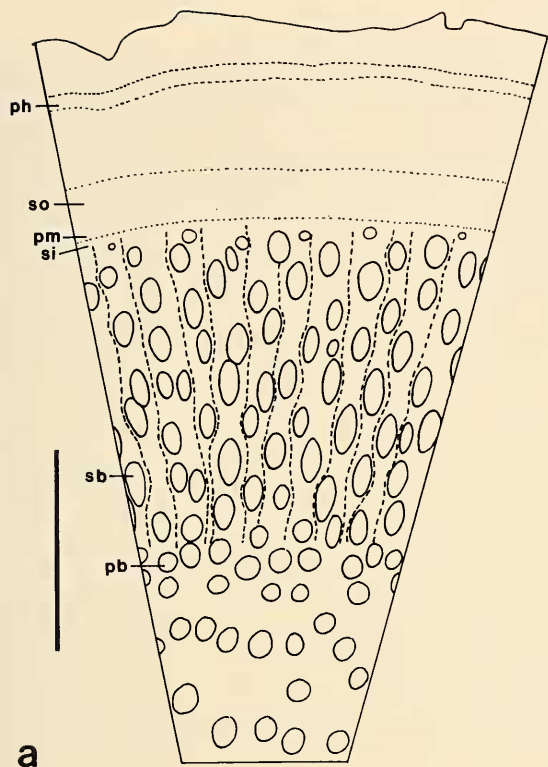
Fig. 2. Diagrams of secondary thickening in *Cordyline stricta*. *lg*, mature lignified ground tissue; *p*, phloem; *pb*, primary vascular bundle at outer limit of primary stele; *ph*, phellogen established under the leaf bases; *pm*, perimeristem; *sb*, secondary vascular bundle; *si*, secondary derivatives of the perimeristem formed on its inner face; *so*, secondary derivatives of the perimeristem formed on its outer face; *x*, xylem.

a. TS sector of outer part of mature stem showing secondary tissues. The radiating broken lines indicate the radial rows of secondary lignified ground tissue laid down by the perimeristem. Scale = 1mm.

b. Schematic representation of the longitudinal aspect of intrusive growth during the differentiation of secondary vascular bundles. Positions 1, 2 and 3 indicate successive stages in the differentiation of a vertical file of perimeristem derivatives into secondary vascular elements. The arrow indicates a horizontal row derived from a particular perimeristem initial, and members of this row in each bundle are labelled t_1 , t_2 and t_3 , and are stippled. At formation (position 1), only one cell of the vertical file is present in the indicated horizontal row (arrow). At position 2, file members have extended to twice their initial length, and intruded halfway into the rows immediately above and below their original position; there are thus two cells at any level in the indicated horizontal row. At position 3, each member of the file now extends through 7 vertical rows, and seven cells will be found in the indicated horizontal row; only three members of vertical file 3 are shown in the diagram for reasons of simplicity.

c. Schematic representation of the transverse aspect of differentiation of secondary vascular bundles. b_1 , b_2 and b_3 indicate three successive stages in the process.

d. TS sector of young stem with perimeristem just differentiated outside the primary vascular bundles. Scale = 1mm.



- i) there is an apparent cutting-up of (i.e., lots of cells divisions in) scattered single derivatives of the perimeristem;
- ii) these strands of cells differentiate into cribricentric (or nearly so) vascular bundles similar in appearance to the primary bundles;
- c) again, the tracheary elements are tracheids of the type described above;
- d) the secondary bundle is formed within one (? always) radial row of secondary tissue;
- e) the secondary parenchyma between the mature secondary bundles becomes lignified, an aspect of the process that will not be discussed further here.

In the longitudinal aspect (RLS) of the secondary tissue it is apparent that there is a great difference between the length of the perimeristem initial and the length of the tracheid that developed from it — indeed from macerated tissue the tracheid is about 20 times the length of the perimeristem initial. Now it can only have attained this length by intrusive growth. Let us look at the process more schematically. In the diagram (Fig. 2b), all the members of the vertical file *I* are destined to become vascular elements; they may be considered protracheary elements. Imagine that we take up a position of inspection at the horizon marked by the arrow. At position 1 in this horizon there is one derivative in the vertical file (t_1). In position 2 each protracheary element of the file has started to elongate apically and basally, and consequently has started to intrude between the cells above and below itself (see cell t_2). The result is that at the given horizon there are now two cells where only one existed before. In position 3 (cell t_3) each protracheary element has elongated to 7 times its original length. Thus at the given horizon our original element (stippled) is now accompanied laterally by six other elements of the same vertical file, three having intruded from above, and three from below; there would be seven elements, therefore, in a transverse section of the file where there was formerly only one. This is *intrusive growth*; what looked like cell-division in the transverse aspect (Fig. 2c) is not. It is this elongation of the tracheids that is responsible for the lateral expansion of the secondary vascular bundle as it matures (cf. b_1 , b_2 and b_3 in Fig. 2c). In macerated secondary tissue (Fig. 3) the tracheids can be seen to be quite twisty and to have battered looking tips as a result of having had to force their way between adjoining elements. Note also that the pitting on these elements is very similar to that on the primary tracheids, being rather like the pitting one usually finds on fibres. The block-shaped lignified parenchyma that occupy the regions between the bundles are also visible in some macerates.

A comparison of macerates from a range of genera possessing this *Dracaena*-type growth is shown in Fig. 3. These are chosen to indicate how similar the elements are, yet they constitute 2-3 different families (depending on author) disposed in 2 different orders.

The seven genera or groups of genera having *Dracaena*-type growth that are recognized in Table 1 have sub-sets of characters that distinguish each from the other. The Aristeae are probably the most out on a limb and are usually referred to the family Iridaceae, which of all the groups we might be considering here has been the most taxonomically stable. But as well as the *Dracaena*-type growth there are other shared character-states that indicate affinity. And this form of growth of stems represents a set of characters that is unlikely to have evolved more than once, and I suggest that it indicates a common origin of those taxa that have it.

Let us look at the world distribution of the generic groups as set out in Table 1. These distributions are compatible with a single origin when the continental masses were together. That is, they appear to be an ancient group that has become differentiated after continental separation.

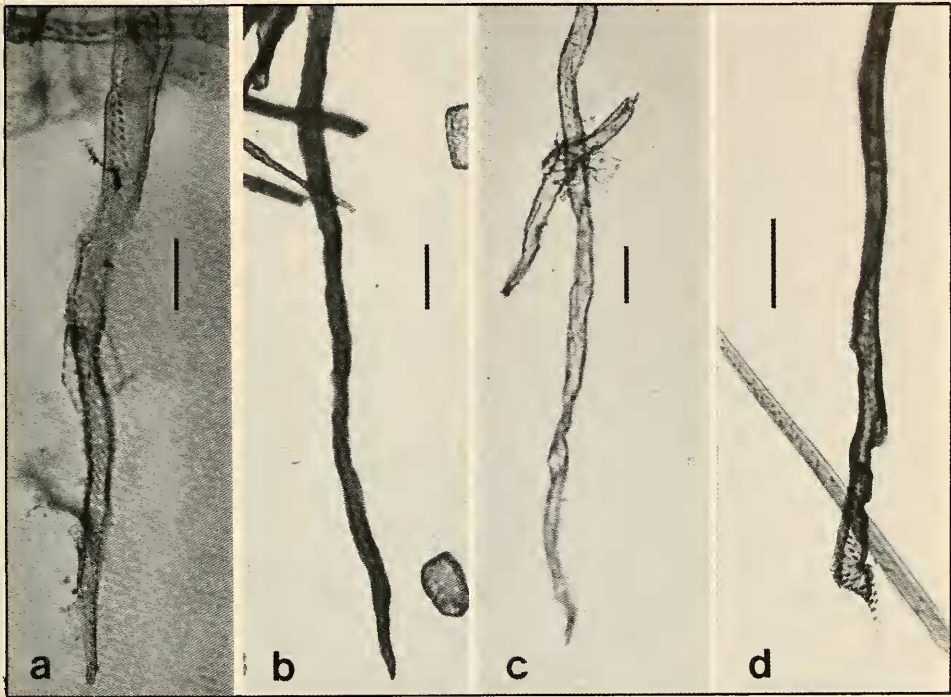


Fig. 3. Xylem tracheids from macerated secondary stem of Dracaenoid plants, showing battered looking tips resulting from intrusive growth. Scale = 100 μ m.

a. *Cordyline stricta*. b. *Aloe* sp. c. *Yucca* sp. d. *Xanthorrhoea australis*.

TABLE 1

Distribution of the taxonomic groups recognizable in the genera displaying dracaenoid thickening

GENERIC GROUP	DISTRIBUTION
<i>Agave</i> and <i>Yucca</i>	Central America
<i>Nolina</i>	North America
<i>Xanthorrhoea</i>	Australia
<i>Aloe</i>	South Africa
<i>Lomandra</i>	Australia, New Zealand, Hawaii
<i>Cordyline</i> and <i>Dracaena</i>	Australia, New Zealand, widespread in the tropics
Aristeae (Iridaceae)	South Africa, Australia

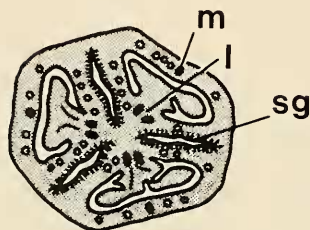


Fig. 4. Median transverse section of ovary of *Xanthorrhoea resinosa* at anthesis. The dorsal or median (*m*) and the ventral or marginal (*l*) vascular traces of each carpel are indicated in black; other vascular bundles (laterals of the dorsal trace) are in outline (see Fig. 5). *sg*, septal gland. Scale = 1mm.

As a group where do they fit is into the lilies *sensu latissimo*. This is where I believe an aspect of floral histology is important. Let us look at some features of the ovary wall. Fig. 4 shows a transverse section of the ovary of *Xanthorrhoea resinosa* in which glands can be seen clearly in each septum of the ovary. A generalized diagram is shown in Fig. 6. The gland is a pouch opening at the top of the ovary and which may extend right to the base of the ovary and even interconnect below the locules. Note also the three-armed stylar canal leading from the stigma to the locules. Similar septal glands occur in the inferior ovary of *Agave* and the superior ovaries of *Aloe* and *Yucca*.

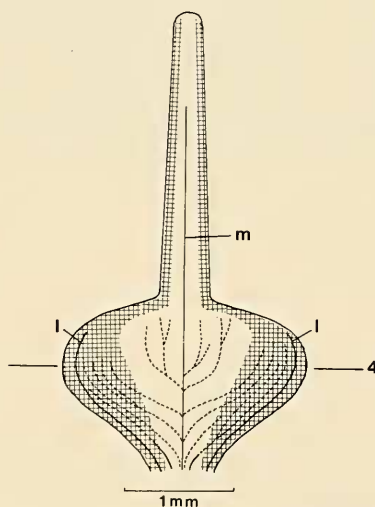


Fig. 5. Diagrammatic reconstruction of a carpel of *Xanthorrhoea resinosa* opened out flat and viewed from the adaxial side. The shaded region indicates the septal portion of the carpel. Note the highly vascularized condition with numerous laterals arising from the dorsal trace (*m*). *l*, ventral or marginal traces. 4 indicates the level of the section illustrated in Fig. 4.

Septal glands appear to occur throughout such groups as Amaryllidaceae (of either Engler or Hutchinson) and Iridaceae, although in some species they appear to have been secondarily lost, and are characteristic of Zingiberaceae, Musaceae, Cannaceae and the syncarpous Palmae. Within the lily family or families their distribution is 'taxonomically sporadic' in current systems. Certainly, Huber (1969) has considered them, but seems to be hesitant/capricious in his taxonomic use of them. Many of these same families are also characterized by a highly vascularized carpel in which the ovary wall is

traversed by laterals arising from the dorsal vascular bundle (i.e., from the mid-vein of the ancestral fertile leaf; Figs 4 and 5). Both septal glands and the highly vascularized carpel are fairly complex characters that indicate a common origin of the plants that bear them.

Well, all the *Dracaena*-type genera have septal glands — this probably is also an ancient character typical of some of the so-called lilialian alliances. It is apparently common in Asphodeloid genera but not in Melanthoid genera. I have no great idea on how systematically significant the presence or absence of septal glands is, but it might be worth considering whether it has any bearing on the evolutionary hypothesis that the monocotyledon flower is a synanthium in origin rather than a strobilus; under this hypothesis each carpel plus 2 stamens is a floral unit subtended by bracts (= perianth).

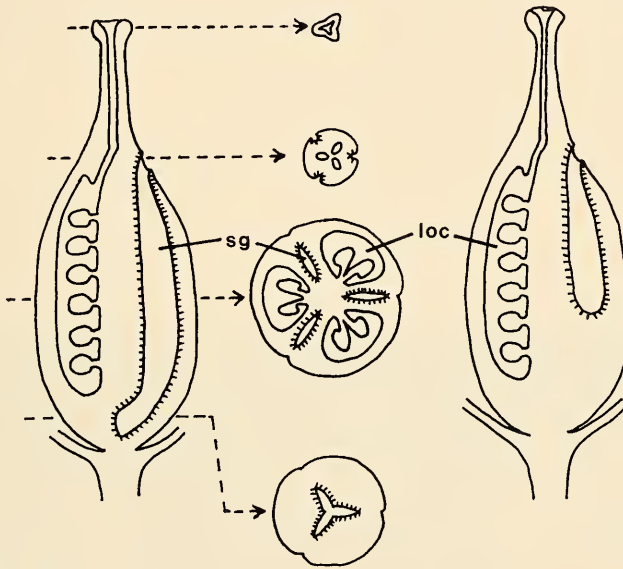


Fig. 6. Generalized diagram of syncarpous gynoecia of *Dracaenoid* monocotyledons showing the septal glands (sg) between the locules (loc) in both longitudinal and transverse aspects.

There is, then, a large group of ancient plants which have *Dracaena*-type growth and septal glands. How do they relate to other lilialian monocotyledons? The following points are of relevance:

1. within the group there are already small species with a vestigial amount of secondary growth
2. outside the group there are small species with vestigial amounts of secondary growth, e.g., *Chlorophytum*
3. all such species have cribri-centric bundles, or collateral bundles with U-shaped xylem consisting of *Dracaena*-like tracheids, whether primary or secondary
4. there are other species with amphivasal bundles, or nearly so, with xylem consisting of tracheids that more or less resemble *Dracaena*-type primary tracheids, but which show no sign of a vestigial perimeristem. All these small species might have septal glands.

In conclusion, there appears to be a series leading to the small perennials with annual re-growth more typical of the temperate regions and much more common in the general botanical literature. But when I speak of an evolutionary series from

arborescent *Dracaena*-type plants to some of the smaller species I don't mean to imply that all the smaller species have come this way. I simply believe that the *Dracaena*-type habit is ancient and the septal gland is probably also old in some of the Lilialian lines. The implication is that other Lilialian genera that do not have these histological characters are not so closely related. The *Dracaena*-type plants are not the ancestors of the lilies *sensu latissimo*. I regret we haven't found a Solomon with his wisdom yet. The problem of elucidating the relationships within this group still remains. If we are to solve it over and above determining the presence or absence of dracaenoid growth, we must:

1. describe properly the tracheary elements. There is pronounced variation from fern-like tracheids in *Dracaena* to those shown in Fig. 3, but a recent publication has them all scored simply as non-vessel elements. The distribution of the various kinds of elements is still a puzzle in the monocotyledons
2. look critically at the bundle types in the stems. Cheadle and Uhl (1948) have too many types, and we must be careful to distinguish between stems, rhizomes and leafy inflorescence axes when making comparisons
3. look for septal glands and multi-veined carpels. Huber (1969) has acknowledged these, but doesn't use data on tracheary elements.

One of the problems that must be overcome is that we must stop thinking of our taxonomy from the top of our hierarchies downwards, and start building up groups from the bottom with what we have at hand. The number of genera involved is so large that no one person can adequately survey them all. If I am going to start on the Sydney scene — with what I have at hand — my groups are going to be incomplete, lack overall world perspective and as a consequence cause, horror of horrors, later nomenclatural and circumscriptive chaos. But start we must, if our treatment of the lilies is to be improved. The remedy, I suggest, is to divorce one's groups from the code and launch them simply so that others can add to or modify them before formalizing them under the code, a procedure that has been adopted quite successfully by Pryor and Johnson (see Pryor and Johnson, 1971) in grappling with the sub-generic taxa in the genus *Eucalyptus*.

References

- BRONGNIART, A. T., 1843. — *Énumération des genres de plantes cultivés au Muséum d'histoire naturelle de Paris*. Paris: Fortin, Masson et Cie.
- CHEADLE, V. I., and UHL, N. W., 1948. — Types of vascular bundles in the Monocotyledoneae and their relation to the late metaxylem conducting elements. *Amer. J. Bot.* 35: 486-496.
- CRONQUIST, A., 1968. — *The evolution and classification of flowering plants*. London: Nelson.
- DAHLGREN, R. M. T., and CLIFFORD, H. T., 1982. — *The monocotyledons: a comparative study*. London: Academic Press.
- ENGELER, H. G. A., and PRANTL, K. A. E., 1897. — *Die natürlichen Pflanzenfamilien*. Nachtrage 1. Berlin.
- HUBER, H., 1969. — Die Samenmerkmale und Verwandtschaftsverhältnisse der Liliifloren. *Mitt. Bot. München* 8: 219-258.
- HUTCHINSON, J., 1934. — *The families of flowering plants*, Vol. 2. London: Macmillan.
- LINDLEY, J., 1846. — *The vegetable kingdom*. London: Bradbury and Evans.
- PRYOR, L. D., and JOHNSON, L. A. S., 1971. — *A classification of the Eucalypts*. Canberra: ANU Press.
- STAFF, I. A., and WATERHOUSE, J. T., 1981. — The biology of arborescent monocotyledons, with special reference to Australian species. In PATE, J. S., and MCCOMB, A. J., (eds), *The Biology of Australian Plants*: 216-257. Nedlands (W.A.): University of Western Australia Press.